



A remarkable diversity of parasitoid beetles (Ripiphoridae) in Cretaceous amber, with a summary of the Mesozoic record of Tenebrionoidea

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ABSTRACT

A diversity of new wedge-shaped beetles (Coleoptera: Ripiphoridae) are described and figured from Burmese amber, representing three new genera and five new species in two subfamilies – Ripidiinae and Pelecotominae. *Amberocula* gen. nov., is the third genus of Ripidiini documented from the Upper Cretaceous (lowermost Cenomanian) amber of northern Myanmar. Three species are included in the genus: *Amberocula muelleri* sp. nov. (type species), *A. costata* sp. nov., and *A. fallax* sp. nov. *Amberocula* is represented by six single male inclusions and one quadruple male syninclusion (for *A. muelleri*). The genus is distinguishable by the combination of number and shape of antennomeres and tarsomeres, reduced mouthparts, and shape of the head, compound eyes, and thorax relative to all extant and fossil members of the tribe Ripidiini. In addition, three single male inclusions and one syninclusion of six males indistinguishable from *Paleoripiphorus deploegi* Perrichot, Nel, and Néraudeau (Ripidiini) are reported. Described syninclusions of both genera support the previous assumption of aggregative-like behavior of male Ripidiini may be a groundplan feature of the tribe and responsible for the presence of such syninclusions. Two monotypic genera, *Plesirotoma alissae* gen. et sp. nov. and *Burmitoma nalaie* gen. et sp. nov., are representative of the subfamily Pelecotominae and are also described and figured. The inclusions represent the second and third definitive records for the subfamily in Cretaceous amber, and also the discovery of fossil pelecotomine females. They differ from the contemporaneous *Flabellotoma* Batelka, Prokop and Engel in the presence of more complete tibial spur formulas and the absence of a ventral abdominal microsclerite. The presence of three species of *Amberocula*, additional material of *P. deploegi*, and two new genera of Pelecotominae demonstrates a surprising abundance of ripiphorids in Cretaceous amber, and we provide comments on the past diversity of this parasitoid family during the period, as well as observations on the nature of their preservation and paleoethology. The known diversity of Mesozoic Tenebrionoidea is cataloged and a key to the Cretaceous diversity of Ripiphoridae is presented.

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1. Introduction

The Ripiphoridae, or wedge-shaped beetles, are a notable parasitoid family of Tenebrionoidea (Coleoptera: Polyphaga: Cucujiformia). The division of the family into subfamilies corresponds to known host associations: roaches (Blattaria) in Ripidiinae, wood-boring beetles (Coleoptera: Ptinidae and Cerambycidae)

in Pelecotominae and Hemirhipidiinae, and aculeate wasps and bees (Hymenoptera: Vespoidea, Apoidea) in Ripiphorinae. Biological data is presently lacking for the basal subfamily Ptilophorinae. Fossils of Ripidiinae and Pelecotominae are known since the Lower Cretaceous and their diversity during this period seems to be much higher than anticipated based on recent discoveries (Batelka et al., 2016b; for placement of *Spinotoma* Hsiao and Huang, 2017: see Supplementary material and Systematic part – Pelecotominae). While the broader record of Tenebrionoidea is significant, it is not as richly documented as has been for Ripiphoridae and its close relative, Mordellidae, and this has an impact on our understanding

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of the geological history of the superfamily as well as the utility of its fossil record for calibrating molecular estimates of diversification. For example, [Toussaint et al. \(2017\)](#) used five Mesozoic fossils assigned to families/genera of Tenebrionoidea and estimated the origin of this clade between the Late Permian and Early Triassic, with a range from 272.03 to 246.86 Ma, a range in sharp contrast to prior work ([McKenna et al., 2015](#)). Obviously, continued revision of past interpretations of tenebrionoid fossils coupled with the discovery of new taxa serves to enhance and refine such estimates, thereby placing considerable importance on systematic studies of past tenebrionoid diversity. The Mesozoic record of Tenebrionoidea has been documented from deposits in China, France, Kazakhstan, Lebanon, Myanmar, Russia, Spain, Switzerland, and U.S.A. with the earliest appearance in the Early Jurassic (see Supplementary material). Some taxa reported in the literature from Mesozoic strata remain of uncertain family placement, such as “*Macrosiagon*” *ebboi* [Perrichot, Nel, and Néraudeau, 2004](#); *Wuhua jurassica* [Wang and Zhang, 2011](#); and *Archaeoripiphorus nuwa* [Hsiao, Yu, and Deng, 2017](#). In addition, some figured or referred specimens are potentially interesting but remain undescribed, such as an aderid from Lebanese amber ([Grimaldi and Engel, 2005](#)), an adult specimen bearing a mosaic of characters of Mordellidae and Ripiphoridae from Canadian Cretaceous amber ([Kaupp et al., 2001](#); [Batelka et al., 2016b](#)), first-instar larvae (triungulinids) from Canadian amber ([Grimaldi et al., 2005](#)), and putative members of Tenebrionidae, Scaptiidae, Melandryidae, Ripiphoridae, and Pyrochroidae from Upper Jurassic–Lower Cretaceous compressions of Liaoning, China ([Kirejtshuk et al., 2010](#)).

Herein we add three new genera and five species to the available record of Tenebrionoidea, specifically among the ripiphorid subfamilies Ripidiinae and Pelecotominae. In addition, we record additional material of *Paleoripiphorus cf. deploegi* [Perrichot, Nel, and Néraudeau, 2004](#) exhibiting putative aggregative behavior, provide a key to the Cretaceous diversity of Ripiphoridae, and provide a summary of Mesozoic tenebrionoid diversity (Supplementary material).

2. Material and methods

2.1. Specimens and preparation

Shortly after our prior contribution on Burmese Ripiphoridae ([Batelka et al., 2016b](#)), an additional eleven pieces of Burmese amber containing male Ripidiinae were provided for our study thanks to the generosity of Patrick Müller (Käshofen, Germany). Where it is necessary and possible, amber pieces were cut to get closer to the beetle inclusions and then polished on a traditional lap, with a final preparation by hand using a fine-grit paste to remove residual microscopic scratches. The material was studied with Olympus SZX12, Olympus BX40, and Zeiss Stereo Lumar V12 stereomicroscopes, and photographed using DP-70 and AxioCam HRm digital cameras attached to the Zeiss Stereo Lumar V12. Additional photographs were prepared with a Canon D550 digital camera mounted on a tripod and coupled with a MP-E 65 mm macro-lens, or attached to an Olympus SZX12. The original photographs were processed using Adobe Photoshop CS4, while some images we prepared a series of focal layers which were then combined using the focus-stacking software packages Helicon Focus Pro or Zerene Stacker. The holotypes are deposited in the Museum für Naturkunde, Berlin, while non-type material (with accession numbers abbreviated as BUB = Burmese Bernstein) is housed in the private collection of Patrick Müller (Käshofen, Germany). Taxonomic actions established here are registered under ZooBank LSID urn:lsid:zoobank.org:pub:95498E3B-3B0D-455F-9C2B-0EB31E0EAF15.

2.2. Outcrop location and age

All specimens examined in this study are preserved in Burmese amber recovered from deposits in northern Myanmar (Hukawng Valley, Kachin) ([Cruickshank and Ko, 2003](#); [Grimaldi and Ross, 2017](#), fig. 1). The age of these deposits has been considered as late Albian or early Cenomanian on the basis of palynomorphs ([Cruickshank and Ko, 2003](#)), and recently confirmed as earliest Cenomanian (98.79 ± 0.62 Ma) by radiometric analysis of zircons ([Shi et al., 2012](#)). The locality has recently been reviewed and mapped by [Grimaldi and Ross \(2017\)](#). Recent investigations on various arthropod lineages has emphasized the tremendous diversity and disparity of the fauna (e.g., [Grimaldi and Ross, 2017](#)), as well as its impact on an understanding of changes in Late Cretaceous biotas along with the Late Cretaceous–Paleogene faunal turnover (e.g., [Grimaldi et al., 2002](#); [Huang et al., 2016](#); [Makarkin, 2016](#)).

3. Systematic palaeontology

Superfamily Tenebrionoidea [Latreille, 1802](#)

Family Ripiphoridae [Gemminge, 1870](#)

Subfamily Ripidiinae [Gerstaecker, 1855](#)

Tribe Ripidiini [Gerstaecker, 1855](#)

Amberocula, gen. nov.

Type species: *Amberocula muelleri*, sp. nov.

Diagnosis. The present genus is known only from males, but based on the universal presence of sexual dimorphism within the subfamily ([Lawrence et al., 2010](#)), females would be expected to be larviform. The genus belongs to Ripidiini owing to the combination of enlarged and strongly faceted compound eye, mouthparts reduced to abbreviated maxillary palpi, antennal flagellomeres with simple and long flattened rami, elytra shortened and widely separated basally, hind wings with strongly reduced venation, abdomen with six tergites and seven ventrites, elongated trochanters, tibiae without spurs, and simple tarsomeres. It differs from all fossil and extant Ripidiini by the combination of 10 antennomeres (scape and pedicel simple; eight flagellomeres, each with a long flattened ramus), maxillary palpi reduced to two separate simple tubercles, 4-4-4 tarsal formula, compound eyes divided by a strip of cuticle completely effaced of ommatidia thereby separating the eye into large upper and lower ocular lobes. The only other genus of Ripidiini with compound eyes completely divided into separate ocular lobes is the extant *Neopauroripidius* [Falin and Engel, 2014](#), which, however, differs from *Amberocula* mainly by having eight antennomeres (with scape, pedicel, and third antennomere simple), developed post-ocular ommatidia, and more complex structure to the mesonotum and metanotum ([Falin and Engel, 2014](#); [Falin et al., 2017](#)). For differences between *Amberocula* and other Cretaceous ripidiines, refer to the key to adults of Cretaceous Ripiphoridae (*vide infra*). In addition, although it cannot be considered as truly diagnostic, it is worth noting that *Amberocula* has the antennae characteristically bent backward in a symmetrical manner (specimens nos. BUB51, BUB75, BUB236, BUB926, MB.I 7290), perhaps the result of the antennae in each of these bordering a section of cuticle effaced of ommatidia. This position of preservation has not been observed in any other Ripidiini entombed in amber.

Etymology. The generic name is a combination of the English noun *amber*, in reference to the material in which all known specimens are preserved, and the Latin noun *ocula* (i.e., “eye”), in reference to its unusually large and divided compound eyes. The gender of the name is feminine. The name is registered under ZooBank LSID

urn:lsid:zoobank.org:act:6D4835CC-09E5-49E0-9D1A-7423D37D0950.

Amberocula muelleri, sp. nov.
(Figs. 1–4)

Holotype. MB.I 7290 (originally BUB927) (Figs. 1, 2A, B); lowermost Cenomanian amber (Shi et al., 2012); Myanmar, Kachin, Hukawng Valley; preserved in a polished, transparent yellow piece of amber (20.2 × 19.5 × 3.0 mm) together with one beetle (Coleoptera: Cleridae); deposited in Museum für Naturkunde, Berlin; *Non-type*

material. BUB53 (Fig. 3A, B) transparent yellow amber (13.1 × 13.4 × 3.1 mm); BUB926 (Fig. 3C, D) transparent yellow amber (17.3 × 11.4 × 2.4 mm); and BUB75 (Fig. 4) syninclusion of four specimens in transparent yellow amber (18.4 × 11.7 × 6.2 mm); deposited in coll. Patrick Müller.

Diagnosis. Elytron 2× as long as wide at widest part; base of antennomeres IV–IX cylindrical; pronotal disc smooth, shallowly convex. Refer also to key (*vide infra*).

Description. Male: Head large, prolonged dorsoventrally, otherwise typical of Ripidiini. Surface of cuticle densely punctate, appearing

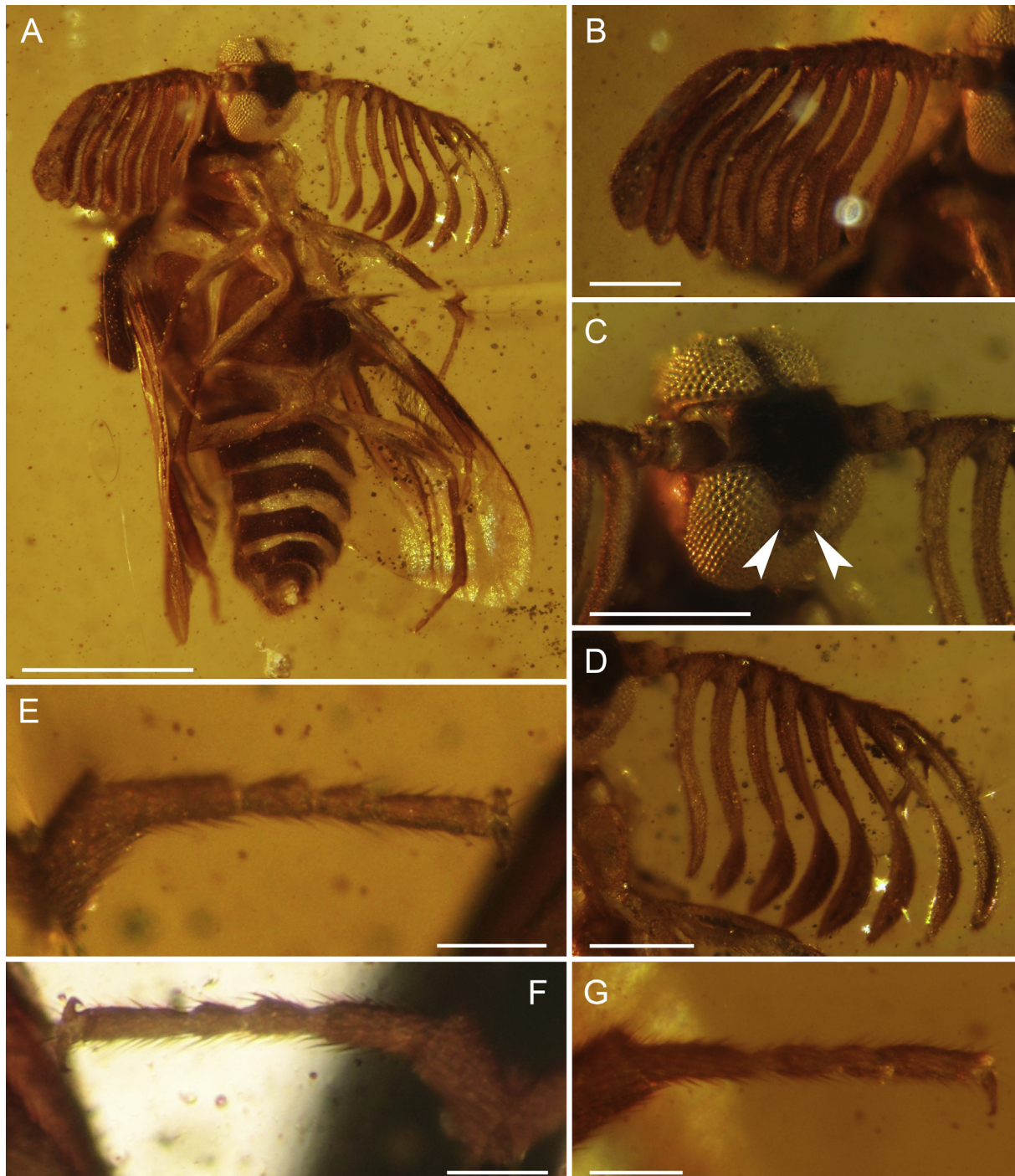


Fig. 1. Male holotype (MB.I 7290) of *Amberocula muelleri* gen. et sp. nov. in Burmese amber. (A) Habitus ventrally. (B) Right antenna ventrally. (C) Head in antero-frontal view; (D) Left antenna ventrally. (E) Protarsus dorsally. (F) Mesotarsus ventrally. (G) Metatarsus dorsally. Scale bars A: 1 mm; B, C, D: 0.5 mm; E, F, G: 0.1 mm.

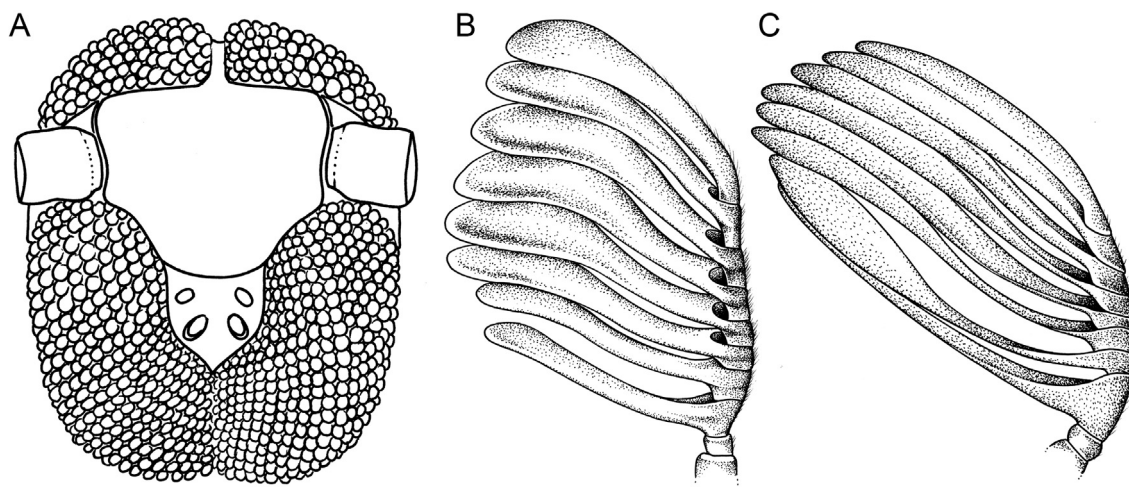


Fig. 2. Drawings of diagnostic structures. (A–B) *Amberocula muelleri* gen. et sp. nov. – head with compound eyes and antenna. (C) *Amberocula fallax* gen. et sp. nov. – antenna. Not in scale.

sub-granular. Frons dark brown, pentagonal in shape, strongly elevated between antennae, with short, erect, dark brown setae (Fig. 1C). Occiput slightly elevated above pronotal disc. Vertex reduced to narrow cuticular strip between compound eyes. Compound eyes large, without visible setae, coarsely faceted, separated into dorsal and ventral ocular lobes by a wide, glabrous strip of integument devoid of ommatidia (Fig. 2A). Dorsal ocular lobes covering almost entire frontal part of head, ventral ocular lobes contiguous ventrally. Postocular ommatidia absent. Mouthparts reduced to maxillary palpi arising under ventral edge of frons, completely surrounded by compound eyes, reduced to small unjointed tubercles. Antennae typical of males of tribe, consisting of 10 antennomeres; antennomere I (scape) robust, cylindrical; antennomere II (pedicel) about one-half length of scape, slightly narrower, oblique apically; antennomere III–IX with long, slightly double-curved rami; base of each successive antennomere becoming gradually longer; antennomere X expanded, similar in shape to rami of previous antennomeres. Antennal rami appear nearly equal in length, gradually widening apically; apices of rami regularly rounded (Fig. 2B).

Pronotum partly covered by whitish, less-transparent resin, bell-shaped, humeral angles rounded, posterior margin nearly straight, pronotal disc slightly concave, coriaceous without impressions; punctures of pronotum similar to that of occiput. Mesonotal disc slightly convex, roughly quadrate from above and as wide as metascutellum, with punctures similar to those of pronotal disc. Metascutellum convex, drop-like, bordered laterally by narrow strip of metascutum. Lateral and ventral aspects of thorax typical of tribe, less well sclerotized than dorsal sclerites, integument weakly and sparsely punctate; setae indiscernible.

Legs typical of Ripidiini; coxae, trochanters, and femora smooth and pale, tibiae and tarsi darker; setae difficult to discern, appearing as suberect, short, and coarse on tibiae and tarsi; apices of tibiae without spurs; tarsi 4–4–4, tarsomeres I–III strongly oblique apically in lateral view, terminal tarsomere more or less cylindrical; pretarsal claws small, simple, straight.

Elytra leathery, widest at midlength; punctation and setation similar to pronotal disc; widely separated, almost concolorous, reaching to about anterior margin of metacoxae when closed, apices widely rounded. Hind wings transparent, highly reflective, covered by microsetae, slightly longer than abdomen and broadest

at about wing midlength, apex with blunt edge; RP distinctly shortened, vanishing about midlength of wing; medial spur extending to posterior wing margin.

Abdomen with six visible tergites, seven visible ventrites; weakly sclerotized with weak punctures and discernible dense setae. Terminal abdominal segment strongly triangular, with long, erect, dense setae.

Measurements. MB.I 7290: Total body length as preserved 3.35 mm; maximum pronotal width approximately 0.6 mm; elytron length 0.75 mm; maximum elytron width 0.45 mm, total length of antenna 1.5 mm, length of first ramus 0.65 mm BUB53: Total body length as preserved 3.0 mm; maximum pronotal length 0.60 mm; elytron length 0.90 mm; maximum elytron width 0.40 mm BUB926: Total body length as preserved 2.9 mm; maximum pronotal width approximately 0.54 mm; elytron length 1.2 mm; maximum elytron width 0.47 mm.

Etymology. The specific epithet honours Patrick Müller (Käshofen, Germany), who disinterestedly provided the type material and many other interesting inclusions for study. The species name is registered under ZooBank LSID urn:lsid:zoobank.org:act:349BD90B-D067-49BE-AB90-3B8F6F175253.

***Amberocula costata*, sp. nov.**

(Fig. 5)

Holotype. MB.I 7291 (originally BUB51) (Fig. 5); lowermost Cenomanian amber (Shi et al., 2012); Myanmar, Kachin, Hukawng Valley; preserved in a polished, transparent yellow piece of amber (14.2 × 12.0 × 7.4 mm) together with nine other insect inclusions (Neuroptera, Hymenoptera, and Diptera); deposited in Museum für Naturkunde, Berlin.

Diagnosis. Elytron 3× as long as wide at widest part; base of antennomeres IV–IX cylindrical; pronotal disc with two deep longitudinal furrows and elevated medial ridge. Refer also to key (vide infra).

Description. Male: Head large, prolonged dorsoventrally, otherwise typical of Ripidiini. Surface of cuticle sparsely punctured, punctures rather minute with interspaces about twice larger than their diameter. Due to preservation, frons and mouthparts not visible. Occiput strongly reduced, elevated, triangular, slightly wider than vertex, head surface nearly completely covered by compound eyes. Vertex reduced to narrow cuticular strip between compound eyes, about as wide as 1.5 width of facets. Compound

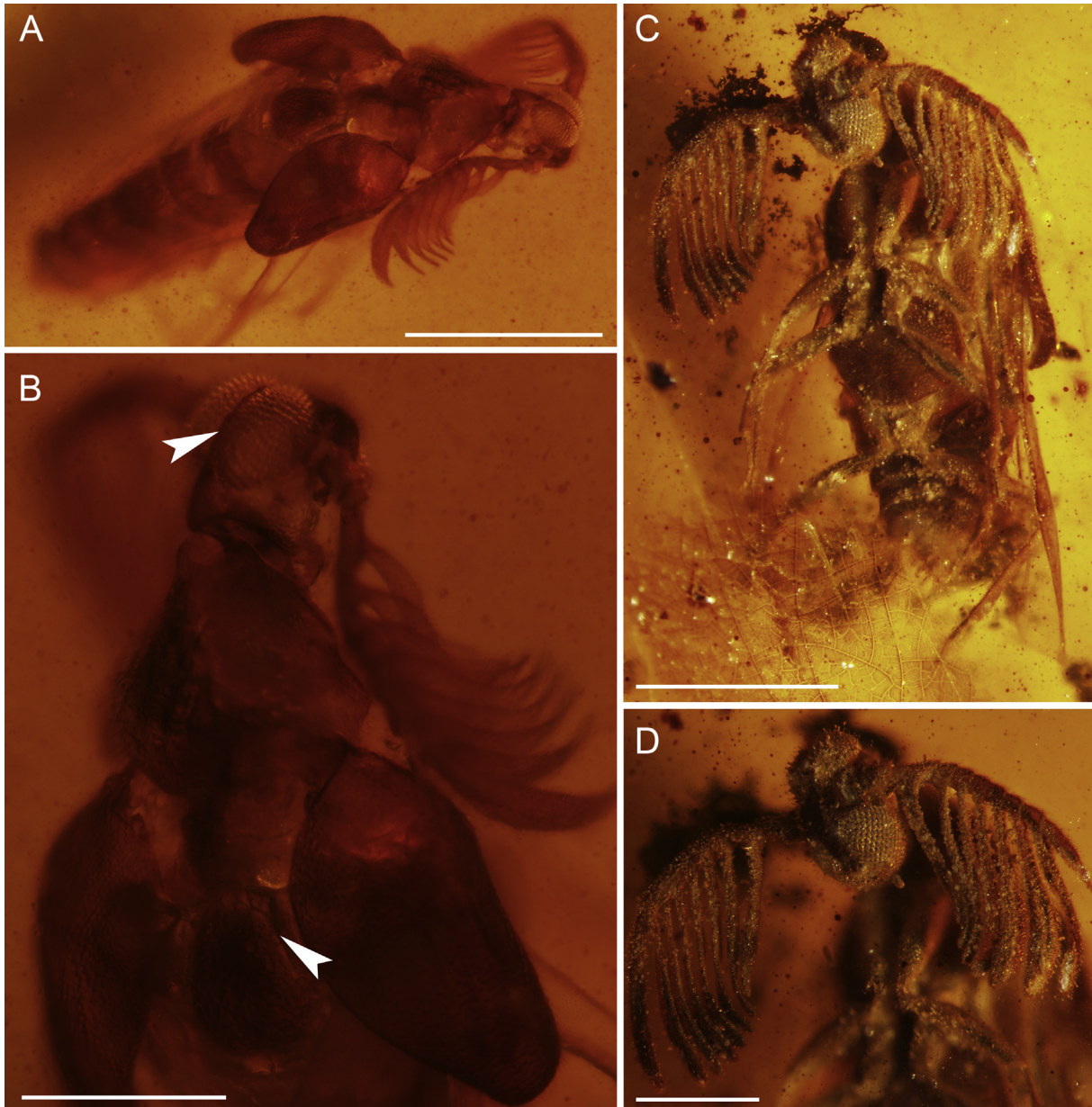


Fig. 3. Two males (BUB53 and BUB926) of *Amberocula muelleri* gen. et sp. nov. in Burmese amber. (A) BUB53 – habitus dorso-anteriorly. (B) Ibidem – detail. (C) BUB926 – habitus ventro-laterally. (D) Ibidem – detail. Scale bars A, C: 1 mm; B, D 0.5 mm.

eyes large, coarsely faceted, covered by dense, pale, erect setae, separated into dorsal and ventral ocular lobes by a wide, glabrous strip of integument devoid of ommatidia. Dorsal ocular lobes covering almost entire frontal part of head, reaching posterior edge of head; aside from reduced occiput, posterior edge of head without discernible cuticle. Postocular ommatidia absent. Mouthparts visible on ventral surface of head as small, unjointed tubercles of maxillary palpi. Antennae typical of males of tribe, consisting of 10 antennomeres; antennomere I (scape) robust, compressed, oblique apically; antennomere II (pedicel) about as long as scape, slightly narrower, strongly oblique apically; antennomeres III–IX with long, slightly double-curved rami; antennomere X expanded, similar in shape to rami of previous antennomeres; base of antennomere III strongly triangular, tapering distally, about twice longer than first and second antennomeres together; all antennomeres covered by short pale

setae; antennal rami appear nearly equal in length, gradually widening apically; apices of rami regularly rounded, lateral edges of rami sclerotized, darkly pigmented.

Pronotum bell-shaped, humeral angles oblique, posterior margin indented from both sides, pronotal disc divided by longitudinal ridges and furrows, two longer ridges bordering longest central furrow starting at base of pronotal disc and reaching posterior edge; posterior width of central furrow slightly wider than mesonotal disc; two shorter ridges starting at middle of lateral edges of pronotal disc and reaching posterior edge at about point corresponding to base of elytra; with longitudinal furrows delimited by longer and shorter ridges and slightly elevated lateral margins of pronotal disc. Mesonotal disc of rectangular shape, slightly concave along midline. Metascutellum obscured by fractures in amber.

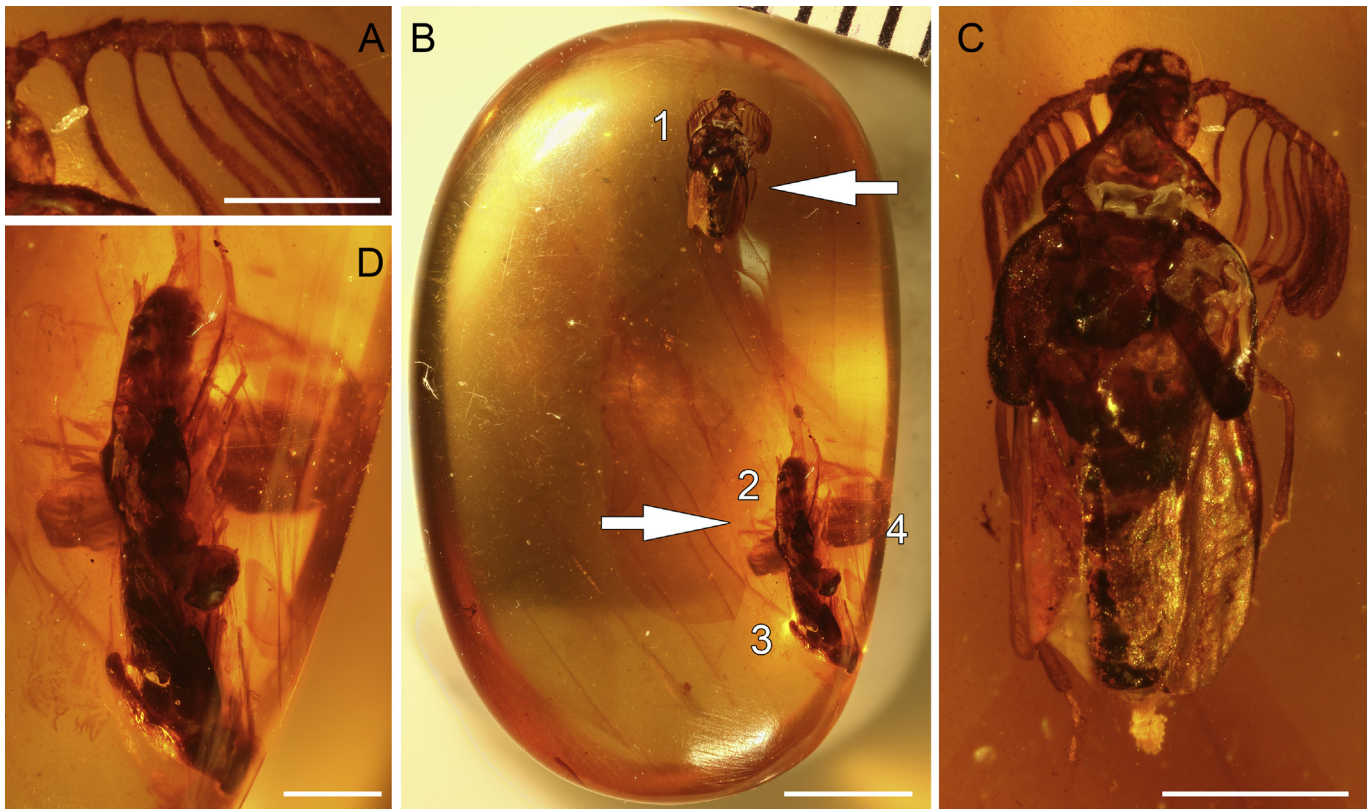


Fig. 4. Syninclusion of four males (BUB75_1–4) of *Amberocula muelleri* gen. et sp. nov. in Burmese amber. (A) Right antenna dorsally. (B) Syninclusion, four entombed specimens indicated by specimen numbers. (C) Habitus of specimen no. 1 dorsally. (D) Specimens no. 2 and 3 touching each other; specimen no. 4 in the background. Scale bars A: 0.5; B: 3 mm; C, D: 1 mm.

Legs typical of Ripidiini; tibiae and tarsi brown; setae difficult to discern, appearing as suberect, short, pale setae; tibiae slightly curved apically, ending by short, strong projections; tarsal formula 4-?-4, tarsomeres I and IV markedly longer, all tarsomeres strongly oblique apically in lateral view; pretarsal claws small, simple, straight.

Elytra leathery, widest at distal third; punctation and setation similar to pronotal disc; widely separated, almost concolorous. Hind wings transparent, highly reflective, covered by microsetae, slightly longer than abdomen and broadest at about wing mid-length, apex rounded; medial spur extending to posterior wing margin.

Abdomen with four visible apical tergites; with longitudinal ridges along midline; apical three ventrites with distinct lateral lobes. Terminal abdominal segment rounded with long, erect, dense setae.

Measurements. MB.I 7291: Total body length as preserved 3.65 mm; maximum head width 0.4 mm; pronotal length 0.90 mm; maximum pronotal width approximately 0.57 mm; elytron length 1.16 mm, width 0.39 mm.

Etymology. The specific epithet refers to the paired longitudinal costae (ridges) bordering deep furrows on the pronotal disc. The species name is registered under ZooBank LSID urn:lsid:zoo-bank.org:act:26956545-ECD3-4718-BDB6-B1AA04709877.

***Amberocula fallax*, sp. nov.**
(Figs. 2C, 6)

Holotype. MB.I 7292 (originally BUB236) (Fig. 6A–C); lowermost Cenomanian amber (Shi et al., 2012); Myanmar, Kachin, Hukawng

Valley; preserved in a polished, transparent yellow piece of amber (15.2 × 14.5 × 5.8 mm) together with two nearly complete apocritan hymenopterans and a nearly complete male of Coccoidea (Hemiptera); deposited in Museum für Naturkunde, Berlin. *Non-type material.* BUB52 (Fig. 6E); lowermost Cenomanian amber (Shi et al., 2012); Myanmar, Kachin, Hukawng Valley; preserved in a polished, transparent yellow piece of amber (43.0 × 28.0 × 9.8 mm) together with one poorly visible Thysanoptera; deposited in coll. Patrick Müller.

Diagnosis. Elytron 2.3× as long as wide at widest part; base of antennomeres IV–IX compressed and adjoining each other; pronotal disc smooth, shallowly convex. Refer also to key (*vide infra*).
Description. Male: Head large, prolonged dorsoventrally, otherwise typical of Ripidiini. Surface of cuticle shining, glabrous (Fig. 6D). Frons dark brown, rectangular in shape, elevated between antennae, dark brown, prolonged ventrally to continue as clypeo-labral strip (Fig. 6D). Occiput slightly elevated above pronotal disc. Vertex reduced to narrow cuticular strip between compound eyes. Compound eyes large, without visible setae, coarsely faceted, separated into dorsal and ventral ocular lobes. Dorsal ocular lobes covering almost entire frontal part of head, ventral ocular lobes contiguous ventrally. Postocular ommatidia absent. Mouthparts reduced to maxillary palpi arising under clypeo-labral strip. Maxillary palpi reduced to small tubercles. Antennae typical of males of tribe, consisting of 10 antennomeres; antennomere I (scape) robust, flattened; antennomere II (pedicel) about one-third length of scape, oblique apically; antennomeres III–IX with long, slightly double-curved rami; antennomere X expanded, similar in shape to rami of previous antennomeres (Fig. 2C). Base of antennomere III strongly

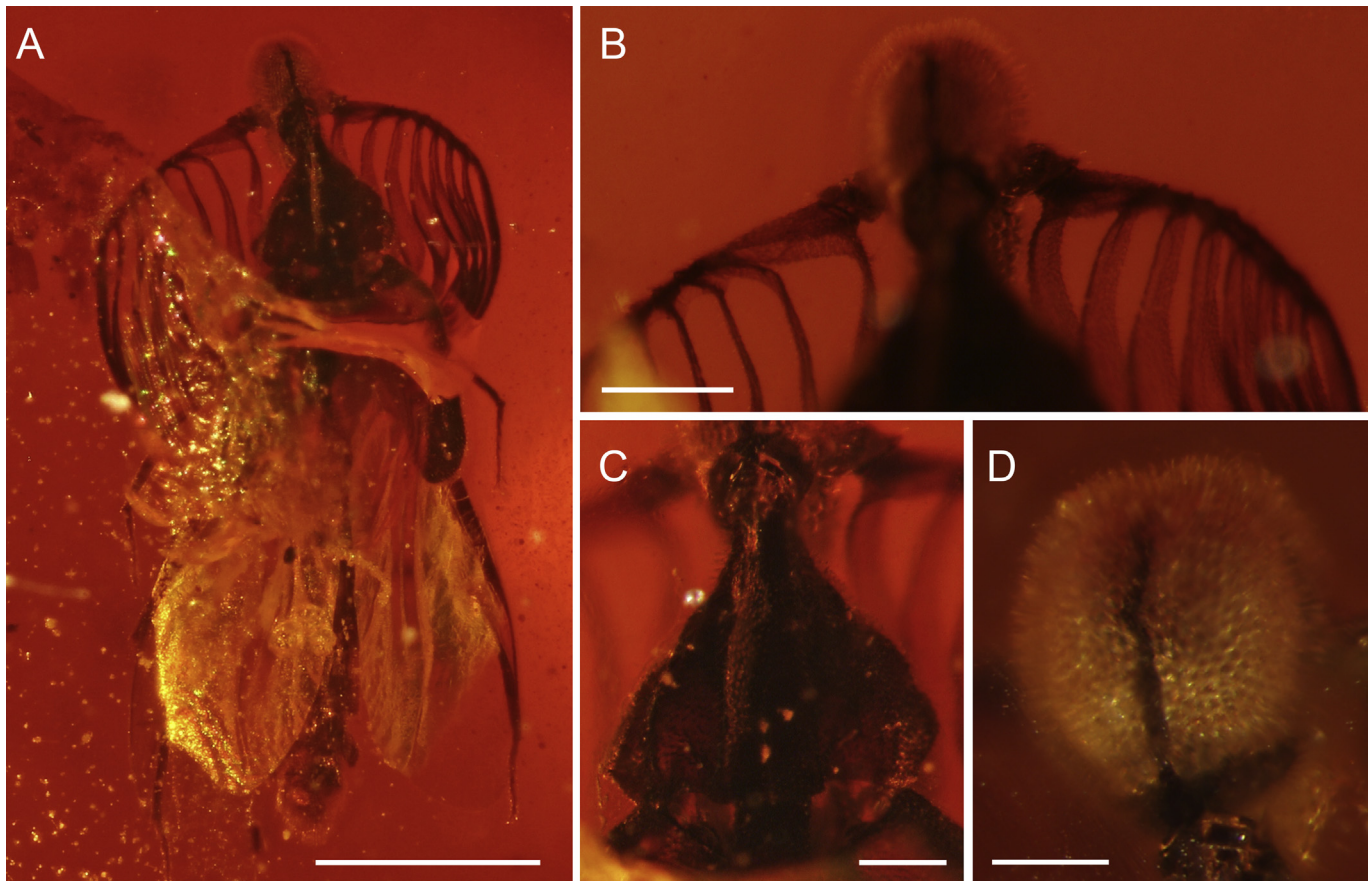


Fig. 5. Male holotype (MB.I 7291) of *Amberocula costata* gen. et sp. nov. in Burmese amber. (A) Habitus dorsally. (B) Detail of basal antennomeres dorsally. (C) Pronotal disc dorsally. (D) head dorsally. Scale bars A: 1 mm; B 0.3 mm; C 0.2 mm; D 0.1 mm.

triangular, tapering distally, slightly shorter than first and second antennomeres together; base of antennomeres IV–IX strongly compressed, three times wider than long, forming profile of antenna compacted (Fig. 6C); antennal rami appear nearly equal in length, gradually widening apically; apices of rami regularly rounded.

Pronotal disc smooth, shallowly convex, bell-shaped, humeral angles acute with apex blunt, posterior margin nearly straight, pronotal disc slightly concave, smooth, without impressions. Mesonotal disc slightly convex, roughly quadrate, as wide as metascutellum. Metascutellum convex ovoid. Lateral and ventral aspects of thorax (in additional specimen) typical of tribe, less well sclerotized than dorsal sclerites, integument weakly and sparsely punctate; setae indiscernible.

Legs typical of Ripidiini; coxae, trochanters, and femora smooth and pale, distal part of tibiae and tarsi darker; setae difficult to discern, appearing as suberect, short, and coarse on tibiae and tarsi; tarsal formula 4-4-4, tarsomeres I–III strongly oblique apically in lateral view, terminal tarsomere more or less cylindrical; pretarsal claws small, simple, straight.

Elytra glabrous, shining, widest about midlength; punctation and setation similar to pronotal disc; widely separated, almost concolorous, reaching about anterior margin of metacoxae when closed, apices widely rounded. Hind wings transparent, highly reflective, covered by microsetae, distinctly longer than abdomen and broadest at about wing midlength, apex rounded; medial spur extending to posterior wing margin.

Abdomen with six visible apical tergites (additional specimen); six visible apical ventrites (holotype), weakly sclerotized with wrinkles. Terminal abdominal segment damaged.

Measurements. MB.I 7292: Total body length as preserved 3.95 mm; maximum head width 0.28 mm; pronotum length 0.88 mm; maximum pronotal width approximately 1.05 mm; elytron length 1.30 mm; maximum elytron width 0.53 mm, length of first antennal ramus 0.90 mm BUB52: Total body length as preserved 5.50 mm; pronotum length 1.05 mm; maximum pronotal width approximately 0.83 mm; elytron length 1.70 mm; length of first antennal ramus 1.60 mm.

Etymology. The specific epithet refers to the fact that at first sight the species can be fallaciously confused with *A. muelleri*. The species name is registered under ZooBank LSID urn:lsid:zoo-bank.org:act:925A5A60-39FF-42BA-9AF5-A46FF06EDB1A.

***Paleoripiphorus* cf. *deploegi* Perrichot, Nel, and Néraudeau, 2004** (Figs. S1 and S2)

Material. BUB930 (Figs. S1A and S1B) preserved in yellow transparent amber (21.2 × 12.8 × 3.0 mm) together with another fragmentary beetle (family unknown); BUB1039 (Fig. S1C) preserved in yellow transparent amber (11.2 × 16.4 × 2.4 mm), BUB1082 (Fig. S1D) preserved in yellow transparent amber (11.1 × 7.3 × 3.0 mm); BUB925 (Figs. S1E and S1F) preserved in yellow transparent amber (22.4 × 18.8 × 5.2 mm) syninclusion with seven males; BUB72 (Fig. S2A and S2B) preserved in yellow transparent piece amber (9.1 × 10.1 × 2.8 mm); BUB1882 (Figs. S2C

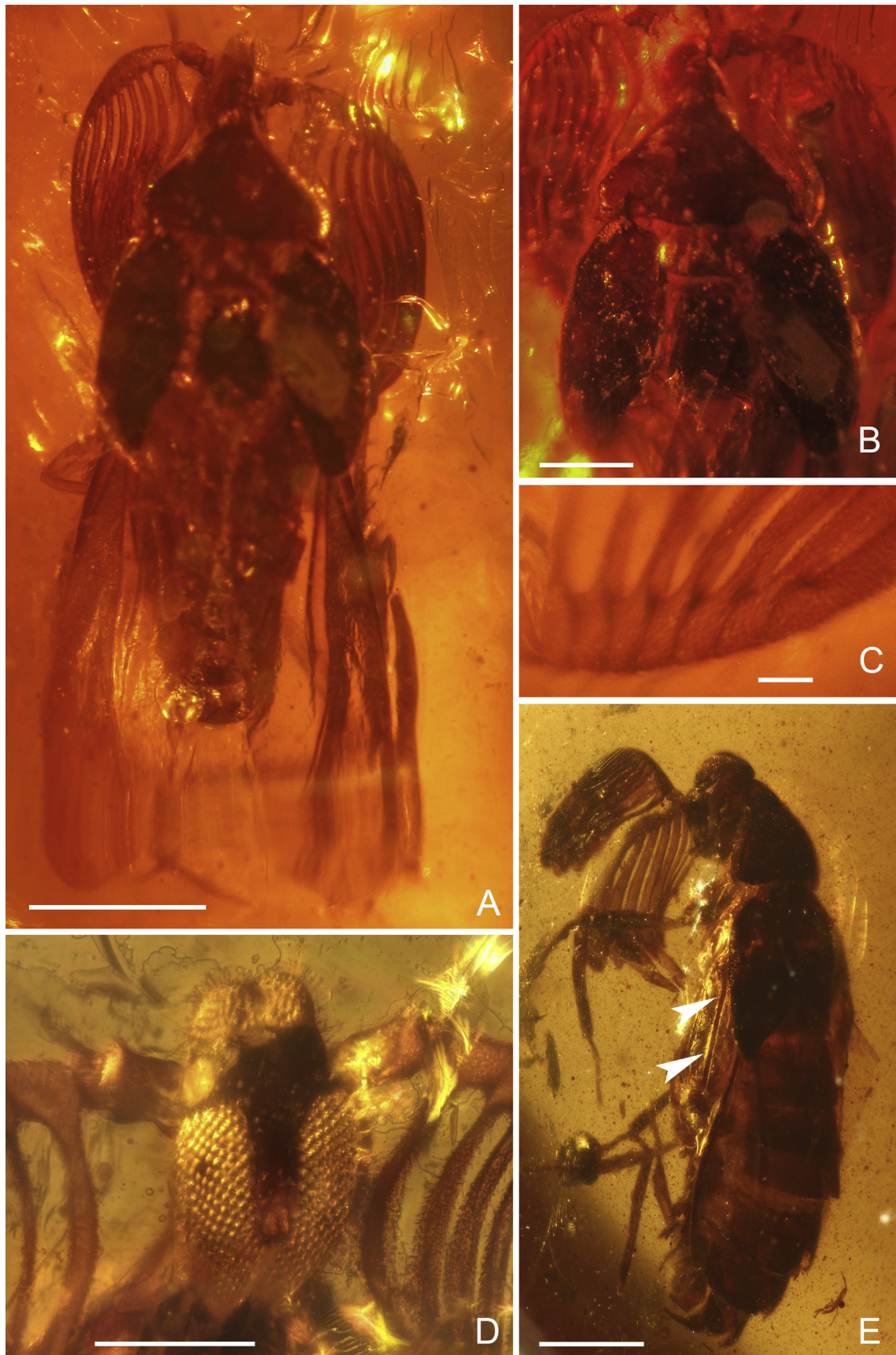


Fig. 6. *Amberocula fallax* gen. et sp. nov. in Burmese amber. (A) Male holotype (MB.I 7292) – habitus dorsally. (B) Ibid – detail of pronotal disc and pterothorax dorsally. (C) Ibid – right antenna ventrally. (D) Surface of cuticle shining glabrous. Frons dark brown, rectangular shape, elevated between antennae of dark brown color. (E) Male (BUB52) – habitus dorso-laterally. Scale bars A, E: 1 mm; B, D 0.5 mm; C 0.1 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

and S2D) preserved in yellow transparent amber (18.9 × 6.4 × 3.7 mm); BUB1881 (Figs. S2E and S2F) preserved in yellow transparent amber (18 × 12.2 × 3.8 mm) syninclusion with two males; BUB929 (Fig. S2G) preserved in yellow transparent amber (13.8 × 12 × 2.7 mm); Cenomanian amber (Shi et al., 2012); Myanmar, Kachin, Hukawng Valley; deposited in coll. Patrick Müller.

Remarks. The genus was described from French Cretaceous amber (uppermost Albian) (Perrichot et al., 2004), and rediagnosed after a new examination of the male holotype by Falin and Engel (2010). Further material of *Paleoripiphorus* from Burmese amber (lowermost Cenomanian) was reported from a series of eight males preserved as syninclusions (Batelka et al., 2016b). A second French specimen from the same outcrop in Charentes from which the holotype was found, was discovered by the application of synchrotron X-ray tomographic microscopy. So far, no confidently diagnostic characters between the French holotype of *P. deploegi* and the specimens in Burmese amber have been distinguished, and the latter material is tentatively attributed to this species.

Subfamily Pelecotominae Seidlitz, 1875

Below presented diagnoses for the two newly established Pelecotominae genera refer only to the genus *Flabellotoma* as the only described fossil member of the subfamily. The genus and species *Spinotoma ruicheni* Hsiao et Huang, 2017 (Myanmar Cretaceous amber), recently described in Pelecotominae, differs from all three fossil and extant Old World pelecotomine genera by distinctly pectinate pretarsal claws and from all known Pelecotominae (including the New World Micholaeminae) by tibiae armed with spines. These characters refers rather to Ptilophorinae than to Pelecotominae (for detail discussion see Supplementary material). Until its redescription and reevaluation of the *Spinotoma*'s characters we retain this genus in Pelecotominae with reservation.

Plesiotoma gen. nov.

Type species: *Plesiotoma alissae*, sp. nov.

Diagnosis. The genus falls among Pelecotominae because of the fully developed mouthparts, elytra covering the entire abdomen and hind wings, and long slender legs with unmodified metatibiae terminated by a dense row of regular, thin, spiniform setae (for a discussion of these features see Batelka et al., 2016b). It differs from all other Pelecotominae by the serrate appearance of the antennae (possibly plesiomorphic, because it is presumed that the non-parasitic ancestor of Ripiphoridae likely possessed simple antennae), while in all extant Pelecotominae the antennae in females bear short or long projections/rami on seven or eight distal antennomeres, so their antennae are pectinate or flabellate in appearance. Moreover, the antennae in *Plesiotoma* consist of only 10 antennomeres (apomorphic), with three basal antennomeres simple, antennomeres IV–IX each bearing a short terminal tooth, and antennomere X elliptical. In all extant Pelecotominae the antennae comprise 11 antennomeres. In contrast to extant genera, the male of *Flabellotoma*, also known from Burmese amber, was described also with only 10 antennomeres, but there was uncertainty surrounding this character state owing to the possible presence of a highly compressed basal flagellomere that could not be confirmed owing to the nature of preservation (Batelka et al., 2016b). Given the presence of an identical character state in *Plesiotoma*, the original observation of only 10 antennomeres in *Flabellotoma* seems to be likely. *Plesiotoma* is also distinguishable by its number of tibial spurs. It shares its 1-2-2 tibial spur formula only with the extant genus *Allocinops* Broun, which is known only from New Zealand (Batelka, 2009), but for which the temples are strongly expanded laterally and the antennae are strongly

uniflabellate in both sexes (Falin, 2003). The tibial spur formula of *Plesiotoma* is only slightly derived from the putatively plesiomorphic state of 2-2-2, a condition which occurs within the subfamily only in another two New Zealand genera, *Rhipistena* Sharp and *Sharpides* Kirkaldy. For a discussion of this character among Pelecotominae, refer to Batelka (2009) and Batelka et al. (2016b).

Spur formulas are consistent among different species of the same genus, but vary widely among the genera of the subfamily. Although the phylogenetic pattern of this character state remains to be investigated, this character has never been observed as sexually variable among Pelecotominae (Batelka et al., 2016b). Therefore, we interpret *Plesiotoma*, despite the many similarities in habitus with *Flabellotoma*, to be a different genus rather than the opposite sex of *F. heidiaea*. *Plesiotoma* also differs from *Flabellotoma* by the absence of a microventrite between the first and second ventrites and the less pronouncedly emarginate compound eyes (Batelka et al., 2016b).

Etymology. The generic name is a combination of the Greek, *plesios* (meaning, “near to”), in reference to putative ancestral state of several key characters, and the suffix *-toma*, in reference to the genus *Pelecotoma*, type genus of the subfamily. The gender of the name is feminine. The name is registered under ZooBank LSID urn:lsid:zoo-bank.org:act:7EDBF67E-3EDD-4F52-B0E1-92F7CDD52617.

Plesiotoma alissae, sp. nov.

(Fig. 7)

Holotype. MB.I 7293 (originally KOM16) (Fig. 7A–J); lowermost Cenomanian amber (Shi et al., 2012); Myanmar, Kachin, Hukawng Valley; preserved in a polished, transparent yellow piece of amber (17 × 8.0 × 6.1 mm); deposited in Museum für Naturkunde, Berlin.

Diagnosis. As for the genus (*vide supra*).

Description. Body elongate, dark brown, integument of pronotal disc with pattern of dense punctures; elytra densely covered by appressed, short, pale setae (Fig. 7H).

Head compressed antero-posteriorly, subglobular (Fig. 7C), left surface completely obscured by a bubble; vertex slightly upraised. Antenna with 10 antennomeres (difficult to discern in holotype, possibly 11, although unlikely); scape (antennomere I) sub-cylindrical, widest at midlength, at least twice length of pedicel; pedicel (antennomere II) elongate, with distal edge oblique; antennomere III simple, cylindrical, basally narrower, slightly longer than pedicel, at least twice wider apically (Fig. 7I); antennomeres IV–IX modified, flattened, enlarged apically (Fig. 7C); antennomeres IV–V triangular, with both edges equal in length; antennomeres VI–IX triangular, with outer edge of each antennomere distinctly longer; antennomere X elliptical, as long as antennomere IX.

Maxillary palpus with three palpomeres, cylindrical, terminal palpomere slightly longer than basal two palpomeres combined, tapered apically. Mandibles, labrum, and labium not discernible (mandibles probably atrophied or reduced to short teeth). Labial palpi minute, filiform, with two palpomeres. Compound eyes large, reaching posterior edge of head (Fig. 7A, C).

Pronotal disc slightly convex, markedly narrower proximally, neck-like; distal corners of pronotal disc with short projections; median lobe of pronotum slightly and continuously convex, with well-discernible impressed line along posterior margin. Mesoscutellar shield rectangular, slightly wider basally (Fig. 7B). Metepimeron, metepisternum, and metasternum not discernible due to preservation. Metathoracic discrien strongly pronounced, appearing as deep furrow.

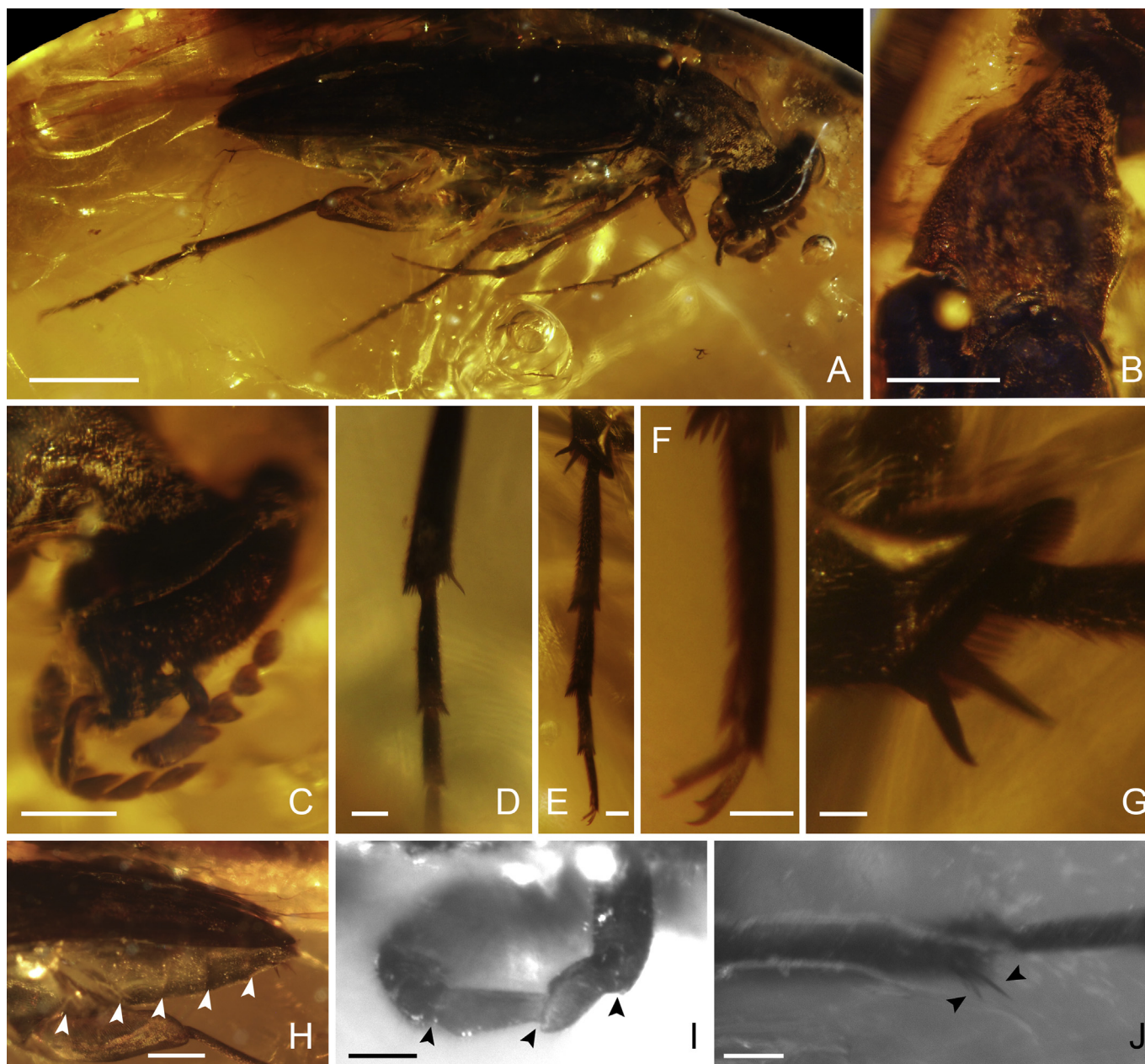


Fig. 7. Female holotype (MB.I 7293) of *Plesiotoma alissae* gen. et sp. nov. in Burmese amber. (A) Habitus antero-laterally. (B) Pronotal disc dorso-laterally. (C) Head ventro-laterally. (D) End of protibia with one apical spur and tarsal segments. (E) End of metatibia with two apical spurs and tarsal segments. (F) Hind leg pretarsal claws. (G) Tibial spurs and apical edge of metatibia in detail. (H) Abdomen ventrally with five visible ventrites. (I) Antennomeres I–III. (J) Tip of mesotibia with two apical spurs. Scale bars A: 1 mm; B, H: 0.5; C: 0.3; mm; D, E, I, J: 0.1 mm; F, G: 0.05 mm.

Elytra elongate, fully covering abdomen and hind wings, well sclerotized, with apices diverging, tapered in width apically, with narrow shoulders as wide as distal width of pronotal disc.

Legs long (Fig. 7A); all femora flattened, slender; all tibiae slightly widened apically, with apex terminated by dense row of regular, thin, spiniform setae (Fig. 7D–G, J); pro-, meso-, and metatibiae with spur formula 1-2-2; tarsal formula 5-5-4 (right legs completely preserved; left meso- and metathoracic legs missing); pretarsal claws bidentate (sharply terminated with marked inner tooth).

Abdomen with five ventrites (Fig. 7H).

Measurements. MB.I 7293: Total body length as preserved 5.45 mm; pronotum length 1.20 mm; maximum pronotal width approximately 1.05 mm; elytra length 3.90 mm; maximum elytron width

0.64 mm; mesoscutellar shield length 0.175 mm, maximum width 0.14 mm mesotarsus length 0.95 mm; metatibia length 1.4 mm; metatarsus length 1.6 mm.

Etymology. The specific epithet honours Alissa Müller, wife of Patrick Müller who made the holotype available for study. The species name is registered under ZooBank LSID urn:lsid:zoo-bank.org:act:BOE2F7A8-B8D1-4021-A7F1-ADC224DEA7C6.

Burmitoma gen. nov.

Type species: *Burmitoma nalae*, sp. nov.

Diagnosis. The genus is similar to *Plesiotoma* in having antennomeres IV–IX serrate (female sexual character), and in the strongly pronounced metathoracic discrimen. *Burmitoma* differs from *Plesiotoma* by the shape of the head with a markedly elevated

occiput, the prolonged labrum with a longitudinal furrow, and by the 0-2-2 tibial spur formula. The same tibial spur formula is known in the extant pelecotomine genus *Clinops* Gerstaecker, in which, however, the head is not elevated, the labrum is not prolonged, the metathoracic discrimen is almost absent, the antennae have 11 antennomeres, and antennomeres IV–IX are distinctly pectinate in females (Batelka, 2005).

Etymology. The generic name is combined from burmite (i.e., the name for the fossilized resin in which the type species is entombed), and the suffix *-toma*, in reference to the genus *Pelecotoma*. The gender of the name is feminine. The name is registered under ZooBank LSID urn:lsid:zoobank.org:act:330B9019-C185-465A-B578-5C0BF556A40A.

***Burmitoma nalae*, sp. nov.**
(Fig. 8)

Holotype. MB.I 7294 (originally BUB 1043) (Fig. 8A–F); lowermost Cenomanian amber (Shi et al., 2012); Myanmar, Kachin, Hukawng

Valley; preserved in a polished, transparent yellow piece of amber (5.1 × 9.0 × 2.1 mm); deposited in Museum für Naturkunde, Berlin.

Diagnosis. As for the genus (*vide supra*).

Description. Body elongate, light brown, integument of pronotal disc with semierect, sparse, thin, pale setae; elytra covered by semierect, thin, brown setae in basal quarter with density similar to that of pronotal disc and markedly increasing in density in distal three fourths of length.

Head compressed antero-posteriorly, subglobular (Fig. 8A, B), vertex conically elevated slightly above pronotal disc. Right antenna with 10 antennomeres, first antennomere (scape) oval, short, robust; second antennomere (pedicel) small, one-third length of scape; third antennomere poorly visible (probably simple, cylindrical, connection between antennomeres III and IV overlaid by basal maxillary palpomeres), base of fourth antennomere elliptical, flattened in dorso-ventral view; first three antennomeres of right antenna dark yellow, remaining antennomeres of both antennae



Fig. 8. Female holotype (MB.I 7294) of *Burmitoma nalae* gen. et sp. nov. in Burmese amber. (A) Habitus ventro-laterally. (B) Habitus dorso-laterally. (C) Distal part of protibia and protarsus. (D) Distal part of mesotibia and mesotarsus. (E) Distal part of metatibia with metatibial spur. (F) Head and pronotum dorsally. Scale bars A,B: 1 mm; C,D,E: 0.1 mm; F: 0.5 mm.

translucent (cleared during preservation); left antenna (in ventral view) with six apical antennomeres visible (base of antenna hidden by mouthparts); terminal antennomere elliptical, slightly narrowed apically, preceding five antennomeres each with prolonged, narrow base and bearing strong, wide tooth. Maxillary palpi probably with three palpomeres, all palpomeres appear flattened, prolonged, probably equal in length. Labrum narrow, prolonged, with longitudinal furrow. Compound eyes globular, with distinct, large ommatidia, deeply incised above antennal torulus, exposed cuticle rounded in diameter equal to about three ommatidia; in lateral view occupying nearly entire head except occiput and labrum; compound eyes separated by strip of cuticle with shallow furrow.

Pronotal disc convex, narrow proximally, wedge-shaped in cross-section; median lobe of pronotum continuously convex, with two well-distinguishable deeply incised impressions; pronotum separated by open V-shaped notopleural suture (angle 110°). Mesoscutellar shield nearly triangular, tapering posteriorly, with longitudinal impression. Metepimeron extremely narrow, posteriorly expanded above metacoxa; metepisternum triangular, tapering posteriorly, three times wider basally; metasternum trapezoidal in profile, as long as metepisternum, proximally bordered by sulcus along full length of metacoxal edge (Fig. 8A, B). Metathoracic discrimen strongly pronounced, appearing as deep furrow (Fig. 8A).

Elytra elongate, fully covering abdomen and hind wings, well sclerotized. Epipleura along entire visible part of elytra.

Legs long (Fig. 8C–E); all femora flattened, slender; all tibiae slightly widened apically, with apex terminated by dense row of regular, thin, spiniform setae (Fig. 8C–E); pro-, meso-, and meta-tibiae with spur formula 0-2-2; tarsal formula 5-5-? (forelegs completely preserved; right mid-leg complete, left with only partly preserved coxa, femur, tibia; metathoracic legs only preserved of femora and right tibia); pretarsal claws bidentate (Fig. 8C).

Abdomen incompletely preserved, overlaid by milky fractures (Fig. 8B).

Measurements. MB.I 7294: Total body length as preserved 4.0 mm; maximum pronotal width approximately 0.60 mm; elytra length 2.55 mm, maximum width 0.7 mm; mesoscutellar shield length 0.22 mm, maximum width 0.08 mm.

Etymology. The specific epithet honours Nala Müller, daughter of Patrick Müller who made the holotype available for our study. The species name is registered under ZooBank LSID urn:lsid:zoo-bank.org:act:43422496-EB1A-426D-BC6B-E58D0840D8BB.

3.1. Key to adults of Cretaceous species of Ripiphoridae

Provided here, is a key to the current diversity of Ripiphoridae documented from Cretaceous deposits. For taxonomic comments on previously described taxa refer to Batelka et al. (2016b). Owing to its uncertain generic and subfamilial placement and the lack of critical characters in the available diagnosis, “*Macrosiagon*” *ebboi* Perrichot, Nel, and Néraudeau, 2004 (in French lowermost Cenomanian amber) is not included in this key. Similarly, the unnamed first-instar larvae reported in the literature from Burmese amber (Grimaldi et al., 2005) and attributed to Ripiphorinae (Batelka et al., 2016b) are similarly not included in the current key. Interestingly, although the shape of antennomeres varies greatly among the Cretaceous Ripiphoridae, almost all taxa described up to present (with some uncertainty in *Flabellotoma* and excluding “*Macrosiagon*” *ebboi*, and *Spinotoma ruicheni*) have 10 antennomeres.

1. Mouthparts fully developed; elytra covering entire abdomen; distal apex of tibiae terminated by dense row of regular, thin spiniform setae; head subglobular; males and females (Pelecotominae, including tentative placement of *Spinotoma*) 2

- Mouthparts reduced to abbreviated maxillary palpi; elytra shortened and widely separated at their base; distal apex of tibiae terminated by sparse setae undistinguishable from remaining leg setation; head globular; males only (Ripidiinae: Ripidiini) 5
- 2. Antennomeres II and III strongly compressed; antennomeres IV–IX with long flattened rami; abdomen with small microventrite inserted between first and second ventrites; tibial spur formula 0-0-0 (only male known) *Flabellotoma heidia* Batelka, Prokop, and Engel, 2016 (monotypic: Myanmar)
 - Antennomeres II and III cylindrical (Fig. 6I); antennomeres IV–IX almost triangular; abdomen without microventrite; tibial spurs present (only females known) 3
- 3. Tibiae provided with spines; pretarsal claws pectinate ... *Spinotoma ruicheni* Hsiao and Huang, 2017
 - Tibiae smooth; pretarsal claws bidentate 4
- 4. Head with unmodified labrum and occiput; tibial spur formula 1-2-2 (Fig. 7D, E, G, J) ... *Plesiotoma alissae*, gen. et sp. nov. (monotypic: Myanmar)
 - Head with elevated occiput and prolonged labrum with longitudinal furrow; tibial spur formula 0-2-2 (Fig. 8C–E) ... *Burmitoma nala*, gen. et sp. nov. (monotypic: Myanmar)
- 5. Compound eyes divided by strip of cuticle completely effaced of ommatidia to separate upper and lower enlarged ocular lobes; maxillary palpi reduced to two separate, simple tubercles or finger-like projection twice as long as wide at base; eight distal antennomeres each with long flattened ramus (*Amberocula*, gen. nov.) 6
 - Compound eyes holoptic, undivided; maxillary palpi reduced to single, fused palpomere (tubercle); eight distal antennomeres of different shape/structure 8
- 6. Pronotal disc smooth, shallowly convex (Fig. 3A, B); elytron 2.0–2.3× as long as wide at widest part; base of antennomeres IV–IX cylindrical or flattened, compressed and tightly adjoining each other; compound eyes without visible setae 7
 - Pronotal disc with two deep longitudinal furrows and elevated medial ridge (Fig. 5A, C); elytron 3× as long as wide at widest part; base of antennomeres IV–IX cylindrical; compound eyes with dense, erect setae ... *Amberocula costata*, sp. nov. (Myanmar)
- 7. Elytron 2.0× as long as wide at widest part; base of antennomeres IV–IX cylindrical (Figs. 1B, D, 2B, 3A); clypeo-labral strip absent (Figs. 1C, 3C) ... *Amberocula muelleri*, sp. nov. (type species: Myanmar)
 - Elytron 2.3× as long as wide at widest part; base of antennomeres IV–IX flattened, compressed and adjoining each other (Fig. 6C); clypeo-labral strip developed (Fig. 6D) ... *Amberocula fallax*, sp. nov. (Myanmar)
- 8. Only seven distal antennomeres with a single, long, flattened ramus each; tarsal formula 4-4-4 ... *Cretaceoripidius burmiticus* (Cockerell, 1917) (monotypic: Myanmar)
 - Eight distal antennomeres with two short, flattened rami each (rami of ultimate antennomere fused into single structure with visible suture); tarsal formula 5-5-4 ... *Paleoripiphorus deploegi* Perrichot, Nel, and Néraudeau, 2004 (monotypic: France, Myanmar – *vide supra*)

4. Discussion

4.1. Mesozoic Ripiphoridae

4.1.1. Systematics

In all three Burmese genera of Pelecotominae, although with some reservation in *Flabellotoma*, (because of tentative position of *Spinotoma* in Pelecotominae (*vide supra*) this genus is excluded

from this part of discussion), the antennae have been observed to have only 10 antennomeres. It is presumed that the 11 antennomeres of extant Pelecotominae is plesiomorphic, which would imply that the condition in these fossils is derived, and perhaps indicative of a relationship among the fossils relative to their modern counterparts. By contrast, serrate antennomeres IV–IX in females of *Burmitoma* and *Plesiotoma* is likely plesiomorphic, as in all extant Pelecotominae female antennomeres IV–IX are always pectinate (i.e., base of each antennomere is prolonged by a finger-like projection). This combination of characters may deserve (at least for *Plesiotoma*) the erection of a new tribe for these taxa. However, until more completely preserved material is discovered in which the basal antennomeres can be more easily discriminated and all of these taxa are included in a cladistic analysis with their modern relatives, we believe such a taxonomic action in regard to suprageneric ranks within Pelecotominae is unwarranted.

4.1.2. Palaeoethology

Aggregations of male Ripidiini have previously been reported for two extant genera preserved in lower Miocene amber of the Dominican Republic (Batelka et al., 2011), and one syninclusion of *P. cf. deploegi* in Burmese amber (Batelka et al., 2016b). Aggregative-like behavior is here further documented for the Cretaceous genera *Amberocula* and *Paleoripiphorus*, further supporting the conclusion that accidental co-occurrence of these males is unlikely, and favors the hypothesis about actual paleo-behavioral circumstances and lek formation in these extinct species. Conspecific syninclusions of Ripidiinae are unique among Mesozoic Polyphaga. Entombed aggregations of male Ripidiini indicate that this behavior is widely distributed across different genera of the subfamily (see also Batelka et al., 2011), and is most probably connected with a complex life strategy and strong sexual dimorphism (females of extant Ripidiini are larviform and flightless). As these aggregations are likely males coming together as a lek in response to emerging females, it is hoped that someday one of these pieces with numerous males may also include a larviform female of the same species.

4.1.3. Diversity in Burmese amber

Three subfamilies are now confirmed from Burmese amber inclusions. Four genera of Pelecotominae (*Burmitoma*, *Flabellotoma*, *Plesiotoma*, and *Spinotoma*, which placement in the subfamily is tentative), three genera of Ripidiinae (*Amberocula*, *Cretaceoripidius*, and *Paleoripiphorus*), and one representative of Ripiphorinae (attributed by Batelka et al., 2016b, based on first-instar larvae reported by Grimaldi et al., 2005) have been documented. Due to the marked morphological intra- and inter-generic differences among Burmese Ripidiinae, the Cretaceous fauna for at least this subfamily must have been remarkably diverse and suggests that further species and genera should be expected across Cretaceous deposits.

4.2. Mesozoic Tenebrionoidea

4.2.1. Diversity

Currently, the Mesozoic record for Tenebrionoidea consists of 34 described genera and 39 species (see Supplementary material), and the number of described species (mostly from Burmese amber) is increasing each year. An evaluation of the available record reveals remarkably that 46% of the diversity (18 species) belongs to Mordellidae, Ripiphoridae, and Mordellidae-like genera. Interestingly, the only two genera with multiple species within the superfamily are recorded for Mordellidae (three species in *Bellimordella*: Liu et al., 2008) and Ripiphoridae (three species in *Amberocula*: vide supra). According to the latest molecular analysis (Batelka et al.,

2016a), Mordellidae appeared as a terminal clade among a non-monophyletic Ripiphoridae. Their molecular results had low support, but a relationship of both families has been long assumed since their first description (for a historical review see Batelka et al., 2016a). It is of note, that molecular data supported a clade of Mordellidae + Ripiphoridae sister to all remaining Tenebrionoidea and Lymexylidae. Lastly, 23% (9 species) of the diversity of Mesozoic tenebrionoids are of the highly specialized parasitoids of Ripidiinae and Pelecotominae. For the proportional representation of each family, refer to Fig. 9.

4.2.2. Abundance

The number of examined specimens shows a preponderance of Mordellidae, Mordellidae-like individuals, and Ripiphoridae (69%, for proportional representation of all families see Fig. 9). This is due to the overwhelming amount of available ripidiine males (50%). A similar abundance of male Ripidiini was observed in lower Miocene Dominican amber, with species of the extant genera *Quasipirhadius* Zaragoza Caballero and *Neorhipidius* Viana (Batelka et al., 2011). Quite remarkably, the number of available specimens of some Dominican and Burmese species may exceed those of extant species. Ripidiini are simultaneously, with one species of Zopheridae, the only taxa among Mesozoic Tenebrionoidea with more than one specimen referred per species.

4.2.3. Mode of fossilization

Our analysis (see Supplementary material) revealed that in compressed fossils there is a relation between mode of fossilization and phylogenetic membership of the preserved specimen. All members attributable to Mordellidae, Ripiphoridae, and Mordellidae-like genera are preserved laterally as compressions, while the remaining genera outside of this clade are preserved dorso-ventrally or with a combination of both modes. We argue that mode of preservation in Mordellidae, Ripiphoridae, and Mordellidae-like taxa is connected with the wedge-shaped body of the fossilized specimens and natural post-mortem positioning of their exoskeleton, common among their extant relatives.

In amber, we can observe some certain tendencies in preservation among different taxa of Ripidiini, caused probably by post-mortem contraction of antennal muscles. For example, the Miocene specimens of *Quasipirhadius* and *Neorhipidius* are predominantly preserved with the antennae parallel-sided below the ventral surface of the head (see six specimens DA01-06 in Batelka et al., 2011, or all three specimens in a triple syninclusion F-436 and F-437 in Wu, 1997); but a few exceptions to this mode of preservation exist, e.g., in the specimen figured in Poinar and Poinar (1999) or specimen F-386 in Wu (1997). Similarly, in most of the available specimens of *Amberocula*, the antennae are characteristically bent backward (see remark in diagnosis of the genus, vide supra). The clade of Mordellidae, Ripiphoridae, and Mordellidae-like genera is the only lineage within Tenebrionoidea in which similar tendencies can be observed and compared because of a sufficient number of available fossils.

A tendency toward a similar post-mortem position can be also observed in Cretaceous conicocephalate primary larvae preserved in Cretaceous amber from Canada (Grimaldi et al., 2005), Myanmar (Beutel et al., 2016), and Siberia (Kathirithamby et al., 2017). These larvae are attributed either to Strepsiptera (Grimaldi et al., 2005; Kathirithamby et al., 2017), or to Ripiphoridae (Beutel et al., 2016, but see; Batelka et al., 2016b); however, there is a consensus that the larvae belong to parasitoid species. In all three described specimens, the legs are bent towards the head in a characteristic position. The position of the legs is a typical post-mortem position for legs in triungulins of the

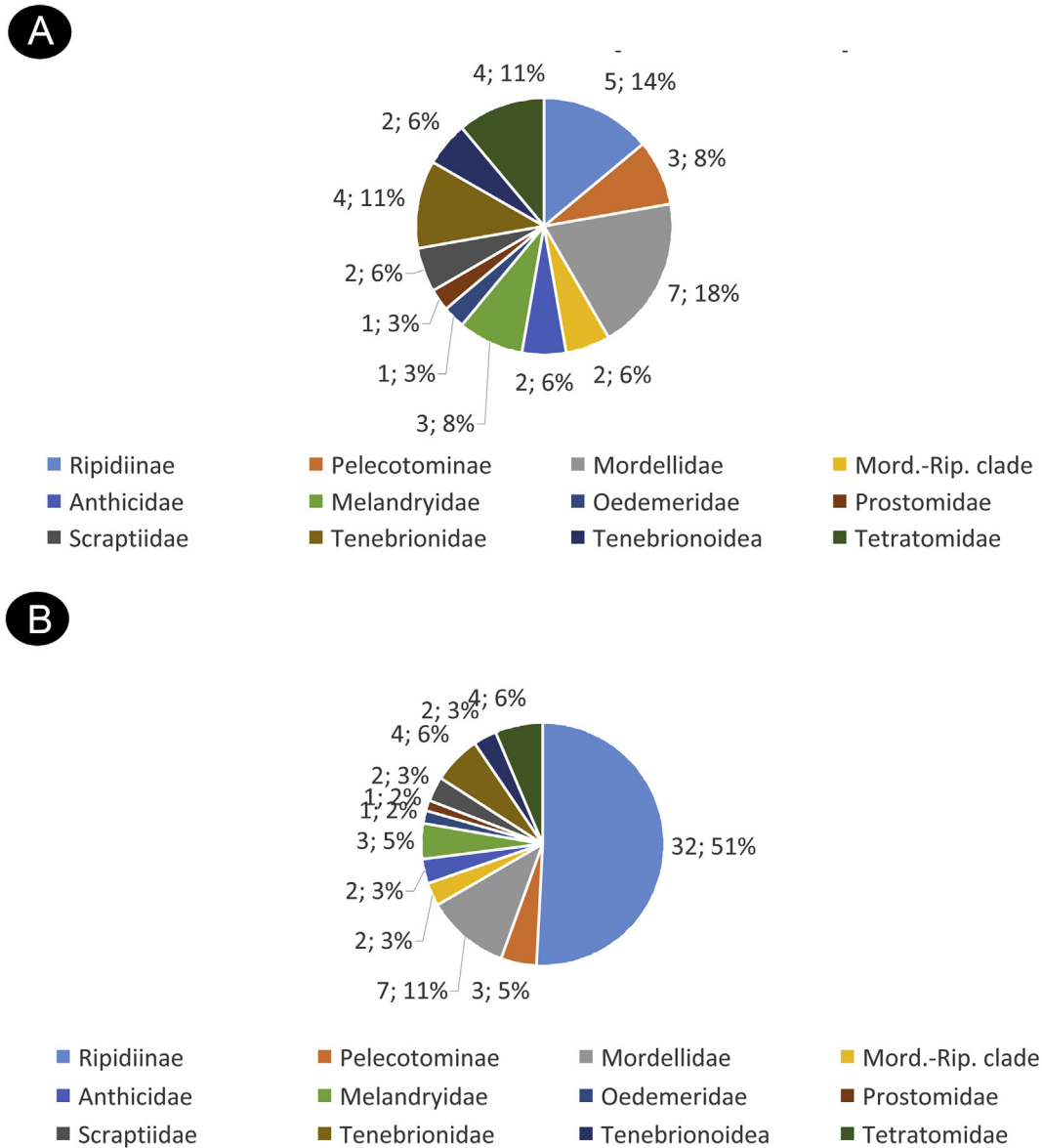


Fig. 9. Diagrams of Mesozoic Tenebrionoidea. (A) By number of known species. (B) By number of recorded specimens.

extant parasitic blister beetle *Meloe (Lampromeloe) variegatus* Donovan, 1793 (see Di Giulio et al., 2014, and Supplementary material, Fig. S4). In *M. variegatus*, a flattened, conical head, similar to the Cretaceous larvae, and its legs of similar proportions and position to the Cretaceous larvae, are apparently adaptations for phoretic behavior. In the meloid, the head is always burrowed toward the host's body and between the metasomal terga of various species of bees, and the legs are bent in a contracted position to support the orientation of the body. It is of note that this “burrowing” phoresy is so far known only for the subgenus *Lampromeloe* (Di Giulio et al., 2014), and therefore “opposite” leg-muscle contractions are probably connected with this unique adaptation to phoresy. This is not to say that the Cretaceous larvae are meloids, but instead highlights the similar morphology and post-mortem orientation of structures between the extant triungulin and the potential paleobiology of the extinct morphospecies. Understanding the predispositions toward fossilization may provide supporting information about morphology or lifestyle for fossil species.

5. Conclusions

A lingering question is whether the outstanding diversity and abundance of Mordellidae, Ripiphoridae, and Mordellidae-like genera in the Mesozoic record of Tenebrionoidea results from a bias in research intensity, or from natural factors reflecting the abundance and diversity of this clade during the period. We argue that at least the abundance (apparently connected with a complex lifestyle) and morphological diversity of parasitoid Ripidiinae supports the notion that this group evolved early and diversified rapidly in the earlier half of the Cretaceous, and that this could be corroborated by more extensive phylogenetic analyses of extant Ripiphoridae combined with node-based dating of diversification events across the family. It is significant that Cretaceous Ripiphoridae show a mixture of a few ancestral characters, unknown in their extant relatives (e.g., simplified meso- and metathorax in *Amberocula*, serrate antennae in female Pelecotominae, two pretarsal segments in Burmese ripiphorine larvae), and a wide array of apomorphies (e.g., divided compound eyes in *Amberocula*, reduced

tarsal formula in *Amberocula* and *Cretaceoripidius*, reduction of antennomeres in both subfamilies, reduction of tibial spur formula in all three genera of Pelecotominae, biflabellate antennae in *Paleoripiphorus*, etc.). Based on available data we are convinced that the parasitoid lifestyle of Ripiphoridae contributed markedly to both the amazing morphological diversity of Pelecotominae and Ripidiinae and to the abundance of male Ripidiini observed in the fossil record.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.cretres.2018.04.019>.